

THE COMPARATIVE MORPHOLOGY OF THE ICACINACEAE II. VESSELS

I. W. BAILEY AND R. A. HOWARD

With six plates

INTRODUCTION

In anatomically primitive xylem of dicotyledons and monocotyledons, the vessel members resemble scalariform-pitted tracheids in size, form and structure, but differ from them in dissolving certain of their pit membranes during the later stages of tissue differentiation. In the secondary body of less specialized dicotyledons, the fusiform initials of the cambium and the scalariform vessel members are relatively long and have extensively overlapping ends. Furthermore, the vessels tend to be isolated from one another and to be more or less uniformly distributed throughout the wood.

The most significant lines of specialization in the vessels of dicotyledons involve (1) conspicuous changes in the size and form of the vessel members, (2) structural modifications of the scalariform pits and the scalariform perforations and (3) a not uncommon tendency for the vessels to aggregate in multiples, chains or clusters. During the first of these major trends of specialization, the vessel members shorten and frequently increase in diameter. As the vessel members shorten and widen, their perforated facets become less and less acutely, and ultimately transversely, oriented. In other words, with increasing specialization of the vessels, their constituent cells become less and less tracheidlike in size and form, Bailey and Tupper (2) and Frost (4 and 5). These changes in the vessels are closely synchronized with concomitant modifications of the cambium, the fusiform initials becoming shorter and elongating less after anticlinal divisions, Bailey (1). In addition, the salient trends of specialization in the size and form of the vessel members frequently are more or less closely paralleled by structural modifications of the perforations and of the pitting of the vessels. The numerous scalariform perforations of the less specialized types of vessels are ultimately replaced by a single, large, elliptical or circular perforation, and the scalariform pits of the non-perforated parts of the vessel members are superseded by smaller pits having first an opposite and subsequently an alternating arrangement, Bailey and Tupper (2), Frost (6).

THE STRUCTURE OF THE VESSELS IN THREE
MAJOR CATEGORIES OF THE ICACINOIDEAE

These salient trends of specialization are well exemplified in the vessels of the Icacinaceae and serve to differentiate the Icacinoideae into various levels of increasing structural modifications. For purposes of the following discussion, it is advisable to segregate the Icacinoideae into three major categories:

I. VESSELS OF BOTH PRIMARY AND SECONDARY XYLEM WITH SCALARIFORM PERFORATIONS

Trilacunar Icacineae

Anisomallon	Cassinopsis	Ottoschulzia
Apodytes	Dendrobangia	Pennantia
Calatola	Emmotum	Pittosporopsis
Citronella*	Oecopetalum	Platea
		Poraqueiba

II. VESSELS OF THE SECONDARY XYLEM WITH SCALARIFORM — POROUS PERFORATIONS

Trilacunar Icacineae

Cantleya	Grisollea	Stemonurus
Discophora	Lasianthera	Urandra
Gastrolepis	Leptaulus	
Gonocaryum	Medusanthera	

III. VESSELS OF THE SECONDARY XYLEM WITH SIMPLE POROUS PERFORATIONS

A. *Unilacunar Icacineae*

Alsodeiopsis	Lavigeria	Merrilliodendron
Desmostachys	Leretia	Pleurisanthes
Humirianthera	Nothapodytes	Rhaphiostylis
Icacina	Mappia	Rhyticaryum

B. *Iodeae (Unilacunar)*

Hosiea	Mappianthus	Polyporandra
Iodes	Natsiatum	

C. *Sarcostigmateae (Unilacunar)*

Sarcostigma

D. *Phytocreneae (Unilacunar)*

Chlamydocarya	Phytocrene	Pyrenacantha
Miquelia	Polycephalum	

In the first of these three categories of the Icacinoideae, the vessels of both the primary and the secondary body are provided with scalariform perforations. The vessel members of the secondary xylem are in general

*In dealing with the genera of the Icacineae we are following the terminology proposed by Howard (7).

very long with more or less extensively overlapping ends, *Figs. 28-31*. The perforated facets of the vessel members tend to be set at a relatively acute angle to the long axis of the vessels. Furthermore, the pitting of the non-perforated facets—except that between vessels and tracheids—is transitional between scalariform and circular-opposite, *Figs. 11-13 and 20-24*.

On the contrary, in the third category of the Icacinoidae, the vessels of the secondary xylem have simple porous perforations, and not infrequently the vessels of the metaxylem are likewise devoid of scalariform perforations. The vessel members are comparatively short and their perforated facets are set either at right angles or at relatively large angles to the long axis of the vessels, *Figs. 47-50*. The non-perforate pits between vessels and between vessels and parenchymatous cells are of the circular-alternating type, *Figs. 17-19*. The walls of the vessels are relatively thick and fused pit apertures are of common occurrence.

The vessel members of the second category, *Figs. 32-45*, of the Icacinoidae are transitional in size, form and structure between the morphologically primitive vessel members of the first category and the highly specialized ones of the third category. Both scalariform and simple-porous perforations occur not only in different vessels of the secondary xylem and in different parts of the same vessel, but also not infrequently at opposite ends of the same vessel element, *Fig. 32*. However, the ratio of scalariform to porous perforations fluctuates greatly in different genera and species and at times in different parts of the same stem.

TABLE I
LENGTH OF VESSEL MEMBERS IN MICRONS

Categories of Icacinoidae	Highest average	Mean of all averages	Lowest average
I. scalariform	2150	1470	950
II. scalariform — porous	1500	1050	700
III. A. porous	750	590	450
III. B-D. porous	600	470	300

As indicated in Table I, the vessel members of Group II are of transitional lengths; the longest-celled species of this group having lengths comparable to the mean of all species in Group I, and the shortest-celled species having averages comparable to the maxima of Group III. The vessel members likewise are of transitional form; those of certain species having perforated facets that are acutely oriented as in Group I and other species having facets that are set at larger angles to the long

axis of the vessels. The pits of the non-perforated facets of the vessels exhibit a wide range of variability, being at times transitional between scalariform and circular-opposite and between circular-opposite and circular-alternate, *Figs. 14-16 and 25-27*.

The vessels in the secondary xylem of most representatives of Group I are numerous, isolated from one another, and more or less uniformly distributed throughout the wood, *Figs. 1-3*.¹ True contacts between different vessels are of infrequent or sporadic occurrence except in certain species of *Pittosporopsis* and *Platea*. In Group III, on the contrary, aggregated vessels or "pore multiples" are of common occurrence, *Figs. 8-10*. As might be anticipated, the distribution of vessels in Group II is transitional and variable; certain species of *Cantleya*, *Fig. 4*, *Stemonurus*, *Fig. 6*, *Lasianthera*, *Leptaulus* and *Gonocaryum* exhibiting relatively few contacts between vessels, whereas species of *Discophora*, *Grisollea*, *Gastrolepis*, *Medusanthera* and *Urandra*, *Fig. 7*, tend to form more or less numerous tangentially, radially or irregularly oriented pore multiples.

Such facts as these demonstrate that there are salient trends of phylogenetic specialization in the vessels of the Icacinaceae which closely parallel those that occur in other families and in the dicotyledons as a whole. Although we have utilized but one of these trends, viz., in the perforations, for differentiating three major categories of the Icacinoideae, such an apparently arbitrary procedure serves to segregate this sub-family into three general levels of increasing structural specialization. That it does so is obviously due to the fact that the various phylogenetic changes in vessels tend in general to be more or less closely correlated.

It should be noted in this connection, however, that the various lines of evolutionary modification are by no means perfectly synchronized. One or more of them may be accelerated when others are retarded or *vice versa*. Furthermore, there are various localized modifications that are divergent from the main trends of phylogeny in vessels. The task of sub-dividing the three major categories of the Icacinoideae into minor levels of structural specialization is complicated by such factors as these. It should be recognized, in addition, that in dealing with minor sub-divisions of a family, where the quantitative and qualitative differences are slight, more attention must be devoted than heretofore to a careful study of the limits of variability within species and in different

¹An appearance of paired vessels in these transverse sections of the wood is due to the fact that certain of the vessels are cut at a level where the ends of the vessel members overlap.

parts of the same plant, Bailey and Faull (3). In the case of tracheary cells, fairly reliable clues regarding the probable limits of structural variability may be secured by comparing the first-formed secondary xylem, obtained from herbarium specimens, with wood cut from mature stems. The vessel members increase more or less in length and in diameter, *Figs. 4-5*, in passing from the first-formed to the later-formed secondary xylem, and the more conspicuous fluctuations in the form of the vessel members and in the character of their perforations and pits are commonly associated with such variations in size.

DETAILS OF STRUCTURAL SPECIALIZATION WITHIN THE THREE MAJOR CATEGORIES OF THE ICACINOIDEAE

GROUP I

The most primitive vessel members of the Icacinoidae occur in the metaxylem and first-formed secondary xylem of *Platea*. The long, slender, extensively overlapping vessel members of such species as *P. excelsa* Bl., *P. latifolia* Bl., *P. parviflora* K. & V. and *P. philippinensis* Merr. have a strikingly tracheidlike form, *Fig. 28*. In tangential view, they have very acutely beveled facets, whereas in radial view they have parallel sides and relatively blunt ends. The numerous scalariform perforations either are distributed throughout the overlapping radial facets of the contiguous vessel members or grade into scalariform pits which they closely resemble in size and form. They are actually membraneless scalariform pits with more or less reduced borders. Where the bordering areas of the secondary wall are much reduced, the pit apertures are large and their outlines nearly coincide with those of the perforations in the primary walls. The intervening "bars" between the pit apertures are slender. On the contrary, where the borders are fully developed the pit apertures are narrower and the intervening bars are wider. The pitting between adjacent vessels is dominantly scalariform, *Figs. 11 and 12*, with occasional transitions to opposite, whereas that between the vessels and the parenchymatous cells fluctuates between scalariform, *Fig. 20*, and opposite.

The smallest vessels of the first-formed secondary xylem of *Platea* are but slightly wider than the largest tracheids, and the larger vessels rarely exceed 50 μ in diameter, whereas those of the later-formed wood may at times attain tangential diameters of from 90-140 μ and radial dimensions of from 130-210 μ . These larger vessel members tend in general to retain a tracheidlike form, *Fig. 29*, in spite of their excessive lateral expansion during tissue differentiation, but some of them become

more or less spindle-shaped in radial view. The perforated facets tend to be less acutely oriented and the scalariform perforations become much extended transversely, viz. at right angles to the long axis of the vessel members. The non-perforate intervascular pits may also attain comparable dimensions, but usually are less extended or are replaced by two or more series of shorter scalariform or oblong pits, *Fig. 12*. The pitting between vessels and parenchymatous cells fluctuates between scalariform and opposite much as it does in the first-formed secondary xylem.

The most highly modified and least tracheidlike vessel members of the Group I Icacinioideae occur in the later-formed secondary xylem of *Emmotum*, *Fig. 31*. Those of *E. holosericeum* Ducke are relatively long, but the ratio of extensively overlapping cells is lower than in the case of comparable material of *Platea*. The vertically as well as transversely enlarged perforations and the broad intervening bars are reduced in number and are localized in a facet that tends to be oriented at relatively large angles to the long axis of the vessel. Where the vessel members overlap more extensively, their ends expand much less during tissue differentiation than do the intervening parts, and therefore extend beyond the broadly elliptical perforated facets as slender projections of varying lengths. The bordered pits in the non-perforate facets which adjoin those of the other vessel members or of parenchymatous cells are circular or elliptical and tend to be arranged in opposite seriation. Typical scalariform pitting is of sporadic or infrequent occurrence.

The narrower vessel members of the first-formed secondary xylem have more acutely oriented perforate facets and less abruptly tapered ends. Although the perforations are smaller and not infrequently more numerous than they are in the larger vessels of the older wood, they are sharply differentiated in size and form from the non-perforate pits. In certain cases, there appears to be a somewhat higher ratio of scalariform and transitional pitting, particularly in vessels in close proximity to the primary body.

The vessel members of the older wood of *Ottoschulzia cubensis* (Wright) Urb. are much smaller than those in comparable material of *Emmotum holosericeum* Ducke, and more nearly resemble those in the earlier-formed secondary xylem of that species. The perforations and broad intervening bars are reduced in number and are localized in a more or less inclined facet that subtends the slender tips of the vessel members. The enlarged perforations are in marked contrast to the small circular or elliptical pits in the non-perforate facets of the vessels.

The remaining representatives of the Group I Icacinioideae exhibit

various transitional stages of phylogenetic modification and various combinations of morphological specialization. The smaller vessel members of *Ocotepealum mexicanum* Greenm. & Thomps., and of *O. guatemalense* Howard, particularly those of the metaxylem and first-formed secondary xylem, have a primitive tracheidlike form and structure comparable to the conditions in *Platea*. The vessel members of the older wood differ, however, from those of comparable material of *Platea* in having a higher ratio of conspicuously tapered ends, i. e. in radial view. Furthermore, the perforations are less numerous and, in the case of the more extensively overlapping vessel members, are localized in a restricted part of the long acutely oriented radial facets. Structural transitions between perforations and scalariform pits are by no means of infrequent occurrence, but scalariform intervacular pitting is less conspicuously developed than in *Platea*. The vessel-parenchyma pits are dominantly scalariform and transitional, and have much enlarged apertures and reduced borders. Thus, they resemble the scalariform perforations in general size and form.

Somewhat similar vessel-parenchyma pitting, *Fig. 21*, occurs in *Poraqueiba sericea* Tul. and serves to differentiate this plant from *Ottoschulzia cubensis* (Wright) Urb. which was formerly included in *Poraqueiba*. It should be emphasized in this connection that the larger vessel members of *Poraqueiba* resemble those of *Ottoschulzia* and of *Emmotum* in having enlarged perforations, but they have broader and less abruptly tapered ends and the perforated facets are more acutely oriented.

The vessel members of the later-formed secondary xylem of *Pennantia* and of certain species of *Apodytes*, e. g. *A. dimidiata* E. Mey., have attained a form which is comparable to that encountered in *Ottoschulzia*. The perforations are localized in broadly elliptical facets, beyond which the more or less abruptly tapered ends of the cells project for varying distances, *Fig. 30*. However, the perforations differ from those of *Emmotum* and *Ottoschulzia* in having vertical dimensions that are not conspicuously greater than the diameters of the small circular bordered pits, and in being separated by slender intervening bars. In these plants scalariform pitting is likewise of somewhat infrequent or sporadic occurrence and has been replaced by numerous small circular or elliptical pits in opposite seriation.

The vessels of *Anisomallon clusiaefolium* Baill. and of *Calatola costaricensis* Standl. and *C. venezuelana* Pitt. also have narrow perforations and slender bars, but the perforations tend to be more numerous and to be localized in longer facets that are more acutely oriented. Further-

more, the vessel members are of more tracheidlike form in that their overlapping ends taper less markedly and abruptly than in the preceding plants. Although the non-perforate pits of the larger vessels are dominantly of the circular-opposite type, there is a higher ratio of vestigial scalariform and transitional pitting, *Fig. 22*. In our material of *Calatola costaricensis* Standl. and *C. venezuelana* Pitt., as also in that of *Dendrobangia boliviana* Rusby there is an unusually high ratio of abnormal reticulate perforations, *Fig. 23*. In such abnormal perforated facets, the smaller oblong or elliptical perforations have either transverse or diagonal seriations.

The vessel members of *Citronella* (including *Briquetina*, *Chariessa*, *Sarcanthidion* and *Villaresia*) and of *Apodytes* fluctuate considerably in size and form, in the number of perforations, in the width of the intervening bars, in the localization of the perforations in facets of varied orientations, and in the ratio of scalariform to opposite pitting, *Figs. 13 and 24*. In certain of these plants, as also in *Cassinopsis tinifolia* Harv., and *Pittosporopsis Kerrii* Craib., the smallest vessel members of the metaxylem and of the first-formed secondary xylem are of approximately as primitive a tracheidlike form and structure as those that occur in *Platea* and *Oecopetalum*.

GROUP II

There are two distinct types of transitions between scalariform and porous perforations in the Group II Icacinoideae. The perforations of *Leptaulus*, e. g. *L. daphnoides* Benth., *L. grandifolius* Engl., and *L. Zenkeri* Engl., fluctuate between 1–12 at each end of the vessel members, *Figs. 39–41*. Where the perforations are more numerous, they vary in form between scalariform, circular and “ephedroid.” It is evident that as the perforations are reduced in number in the broader vessels of the later-formed wood, they become larger and are separated by wider intervening bars. Thus, in the genus *Leptaulus*, the simple porous type of perforation results primarily by reduction in the number, and a concomitant increase in size, of the individual perforations. Although the vessel members are relatively small, having diameters of only 45–75 μ , in the old wood of *L. daphnoides*, they do not retain a tracheidlike form, *Fig. 39*. The perforations are localized in inclined facets that subtend the slender, abruptly tapered tips of the vessel members. The small, circular or elliptical, intervascular and vessel-parenchyma pits are loosely and somewhat irregularly distributed. Typical scalariform pitting tends to be restricted largely to the primary body.

In all of the other genera of the Group II Icacinoideae, the simple

porous condition arises from scalariform types by the elimination of the more or less numerous bars between the scalariform perforations; or, to express the matter ontogenetically, by the cells not forming such secondary wall thickenings during tissue differentiation. Many transitional stages in the elimination of the bars occur within the vessels of the same stem, *Figs. 34-36 and 38*. Furthermore, as previously stated, the ratio of scalariform and transitional to porous perforations fluctuates greatly not only within different species but also in different parts of the same plant. In general, the number of scalariform and transitional perforations tends to be somewhat higher in the first-formed than in the later-formed secondary xylem.

The highest ratios of scalariform and transitional perforations occur in the first-formed secondary xylem of various species of *Stemonurus*. The vessel members are relatively long and slender, and tend to have smoothly tapered ends. The perforations are localized in restricted areas of the overlapping ends of the vessel members and thus occur in facets that are acutely oriented, *Fig. 32*. The more or less infrequently occurring simple porous perforations are oblong or narrowly elliptical and correspond in size and form to the outlines of the complexes of scalariform or transitional perforations. As the vessel members increase in diameter in subsequently formed secondary xylem, their ends become more abruptly tapered and their perforations are localized in facets that are less steeply inclined. The simple porous perforations commonly are more numerous than in the first-formed secondary xylem and are oval, broadly elliptical or circular. The intervascular and vessel-parenchyma pitting fluctuates between scalariform, opposite and alternate and the ratios of scalariform and oblong to elliptical and circular pits vary considerably not only in different species but also in different parts of the same stem. Aggregations of vessels or pore multiples are of relatively infrequent or sporadic occurrence in most species of *Stemonurus*, *Fig. 6*.

On the contrary, the vessels of *Medusanthera* and of *Grisollea Thomassetii* Hemsl. tend to aggregate in small radially, diagonally or tangentially oriented clusters. There is a lower ratio of scalariform and transitional types of perforations in the vessels of these plants, even in those of the first-formed secondary xylem, *Figs. 34-36*. The form of the vessel members and of the simple porous perforations fluctuates between the first-formed and the later-formed secondary xylem much as it does in *Stemonurus*. Even in species which have relatively slender vessels in the later-formed secondary xylem, the vessel members have a high ratio of abruptly tapered ends and perforate facets that are set at relatively large angles to the long axis of the vessels, *Fig. 33*. The inter-

vascular and vessel-parenchyma pits are numerous and relatively small as in *Stemonurus*, but there appears to be a somewhat higher ratio of alternate pitting in *Medusanthera*.

The vessels of *Discophora*, *Gastrolepis*, *Urandra* and *Cantleya* may be differentiated from those of the preceding plants by the large size of their intervacular, *Fig. 14*, and vessel-parenchyma pits, *Fig. 26*. The latter pits vary considerably in size, form and orientation and tend to have more or less enlarged apertures. At times, particularly in the smaller vessels of the first-formed secondary xylem, they are scalariform and resemble the vessel-parenchyma pits that occur in *Occopetalum* and *Poraqueiba* of the Group I Icacinioideae. The ratio of pits with conspicuously enlarged apertures fluctuates considerably in different species and not infrequently in different parts of the same stem. The intervacular pitting varies between scalariform, opposite and alternate, *Figs. 14 and 15*. The size and form of the vessel members, *Fig. 37*, also fluctuate considerably in different species and in different parts of the same plant, as do the size and form of the simple porous perforations, the ratio of scalariform, *Fig. 38*, to simple perforations, *Fig. 37*, and the number and size of the bars in the scalariform and transitional perforations. The vessels of *Cantleya corniculata* (Becc.) Howard have an isolated distribution, *Fig. 4*, whereas those of *Discophora*, *Urandra*, *Fig. 7*, and *Gastrolepis* tend to be aggregated in more or less conspicuous radially, diagonally or tangentially oriented clusters.

The vessels in herbarium material of *Lasianthera africana* Beauv. are isolated. The vessel-parenchyma pits are scalariform with enlarged apertures and thus resemble those that occur in the four preceding genera, but the intervacular pits are small and resemble those that occur in *Stemonurus* and *Medusanthera*. The vessels of *Gonocaryum* also have an isolated distribution and numerous small intervacular pits. However, the vessels of this genus differ from those of all of the preceding genera in the much modified and abnormal form of their scalariform perforations, *Figs. 43-45*, which frequently are vertically, diagonally, concentrically or irregularly, rather than transversely, oriented. The small simple porous perforations tend to be broadly elliptical or circular even in the vessels of the earlier-formed secondary xylem and are localized in small more or less inclined facets that subtend the abruptly tapered ends of the vessel members, *Fig. 42*. The intervacular and vessel-parenchyma pitting is transitional between circular-opposite and circular-alternate, *Fig. 27*, and typical scalariform pitting is of sporadic or vestigial occurrence except in close proximity to the metaxylem.

GROUP III

As shown in Table I, the vessel members of the Icacinoideae tend to shorten with increasing structural specialization of the vessels. That they tend to widen is indicated in Table II.

TABLE II
DIAMETER OF LARGEST VESSELS IN MICRONS

Inner Secondary Xylem	Group I	Group II	Group III
Less than 40 μ	50%	50%	9%
40-65 μ	50%	50%	28%
More than 65 μ	0%	0%	63%
Outer Secondary Xylem			
Less than 100 μ	40%	22%	5%
100-125 μ	44%	34%	10%
More than 125 μ	16%	44%	85%

This tendency is detectable in the outer secondary xylem of the Group II Icacinoideae, but is not statistically demonstrable without additional data in the first-formed secondary xylem. On the contrary, it is clearly exemplified in both the inner and the outer secondary xylem of the Group III Icacinoideae. That the conspicuous enlargement of the vessels in the first-formed secondary xylem of Group III Icacinoideae is commonly associated with the acquisition of a scrambling or vinelike habit of growth is demonstrated in Table III. It occurs not only in the tribes Iodeae, Sarcostigmataeae, and Phytocreneae, but also in scandent species of such genera of the unilacunar Icacineae as *Lavigeria*, *Leretia*, *Pleurisanthes* and *Rhyticaryum*, and to a lesser extent in certain species of *Humirianthera* and *Rhaphiostylis* which have a scrambling habit of growth. Therefore, in dealing with the Group III Icacinoideae, it is essential to differentiate between trends of specialization in plants of different habits of growth.

TABLE III
DIAMETER OF LARGEST VESSELS IN MICRONS

Group III:	Trees - Shrubs	Scrambling Shrubs	Vines - Lianas
Inner Secondary Xylem			
Less than 40 μ	35%	0%	0%
40-65 μ	58%	33%	12%
More than 65 μ	7%	67%	88%

In the arborescent and frutescent species of *Alsodeiopsis*, *Mappia* and *Nothapodytes*, the vessels tend to occur in radial clusters, *Fig. 8*, or at

times in more extensive, loose, radial grouping. The largest vessels of the first-formed secondary xylem fluctuate in diameter from 30–65 μ , whereas those of the later-formed secondary xylem attain tangential diameters of from 80–170 μ . Vestiges of scalariform perforations and of scalariform or opposite intervacular pitting are confined to the metaxylem. The vessel members, *Fig. 47*, vary considerably in form, those of smaller diameter having more acutely oriented perforate facets and less abruptly tapered ends. The vessels of *Desmostachys Vogelii* Stapf fluctuate similarly in size and in the form of their constituent cells, *Fig. 46*, but differ from those of the preceding genera in tending to occur in tangential, *Fig. 9*, rather than in radial groupings. There is, in addition, a much higher ratio of scalariform perforations in the metaxylem of both *Desmostachys Vogelii* Stapf and *D. Preussii* Engl. The vessels of *Merrilliodendron* are much reduced in number, but are of relatively large size, attaining diameters of from 70–90 μ in the first-formed secondary xylem and as much as 250 μ in the later-formed wood. The widely spaced vessels occur singly and in occasional tangentially, diagonally or radially oriented clusters. The pitted vessels of both the metaxylem and the secondary xylem have prevailing porous perforations. The vessel members, particularly of the outer secondary xylem, have a much higher ratio of transversely oriented perforate facets, *Fig. 50*.

The young stems¹ from herbarium specimens of scrambling or vine-like Icacinaceae are either of normal structure or exhibit more or less conspicuous "anomalous" features. Thus, in our material of *Humirianthera ampla* (Miers) Baehni, *H. rupestris* Ducke, *Icacina Mannii* Oliv., *I. senegalensis* A. Juss., *Rhyticaryum elegans* Schellenb., and *R. onocarpum* Sch. & Lautb., the internodal parts of the stem have a nearly cylindrical form. The vessels of the secondary xylem, although exhibiting a tendency to occur in loosely organized tangential or concentric grouping as in *Desmostachys*, are more or less uniformly distributed around the stem. They attain maximal diameters of from 50–80 μ . On the contrary, in comparable material of *Leretia*, *Pleurisanthes* and *Rhaphiostylis*, the secondary xylem frequently develops precociously upon opposite sides of the stem, i. e., between the orthostiches. The vessels of the secondary xylem, which attain diameters of from 65–120 μ , tend to aggregate in the more rapidly growing sides of the stems. These tendencies towards "anomalous" types of growth are much exaggerated in the stems of various species of *Pleurisanthes*, which during subsequent growth assume a form similar to that of *Iodes ovalis* Bl., illustrated in

¹Unfortunately, material from older stems of many of these plants is not available at present.

Fig. 7 of the preceding paper of this series. The precociously developed, large-vesselled secondary xylem differs, however, from that formed in comparable material of *Iodes ovalis* in having numerous strands of included phloem. In *Lavigeria salutaris* Pierre, the large-vesselled secondary xylem develops on all sides of the internode and is formed by successive cambia. There appears to be a much lower ratio of vestigial scalariform perforations in the metaxylem of *Lavigeria* and *Pleurisanthes* than in that of *Leretia*, *Rhaphiostylis*, and particularly of *Humirianthera* and *Icacina*.

Enlargement of the vessels in the first-formed secondary xylem, *Fig. 10*, coupled with conspicuous "anomalous" types of structure, occurs characteristically in the Iodeae, Sarcostigmateae, and Phytocreneae and has been adequately illustrated in the first paper of this series. *Mappianthus* and *Sarcostigma* are exceptional in having a normal cylindrical secondary body and vessels that are not aggregated between the orthostiches. *Sarcostigma* is characterized, in addition, by having numerous strands of intraxylary soft bast and vessels that are arranged in loose radial groupings. Furthermore, we have called attention in our preceding paper to the fact that in *Hosiea sinense* (Oliv.) Hemsl. and *Iodes liberica* Stapf, the young stems are extraordinarily variable; certain of them having small vessels that are localized in distribution and others having large vessels that are more or less uniformly arranged around the stem.

In most of the Iodeae, Sarcostigmateae and Phytocreneae, the pitted vessels of the metaxylem have exclusively porous perforations. There commonly is a higher ratio of vessel members with slightly inclined or transversely oriented perforate facets in both the metaxylem and secondary xylem, *Fig. 49*, of these plants than there is in a majority of the unilacunar Icacinaceae. The most highly specialized vessels of the Icacinoidae occur in various representatives of the Phytocreneae. The larger vessels frequently are composed of very short members which are broader than long, have truncated ends and are devoid of projecting tips, *Fig. 48*. These plants also form curious slender, "fibriform" vessel members in the much modified outer part of the primary body.

DISCUSSION

The data recorded in the preceding pages indicate that there are clearly defined trends of specialization in the vessels of the Icacinoidae. Most of these lines of phylogenetic modification are irreversible and parallel those that occur in other families of the dicotyledons. Thus, it is possible to differentiate the Icacinoidae into various levels of

increasing structural specialization. That such levels of specialization may be of some taxonomic, as well as of purely phylogenetic, interest is suggested not only by the general grouping of genera and tribes within our three major categories of the Icacinoidae, but also by the fact that all of the Icacinaceae in Group III have unilacunar nodes whereas those in Group I and II have trilacunar ones. It should not be inferred from this, however, that all of the genera in one of these categories are necessarily more closely related genetically to one another than to genera in the other categories. Parallel development and convergent evolution are of such common occurrence in foliar and cauline, as well as in floral, structures that evidence from all parts of the plant must be harmonized and integrated in attempting to determine actual genetic affinities within an order, family, sub-family or tribe. Therefore, a discussion of the taxonomic implications of the data presented in this paper should be deferred until we have completed our investigations of other tissues and organs of the Icacinoidae.

SUMMARY

1. A study of the vessels reveals salient irreversible trends of structural specialization in the Icacinaceae which parallel those that occur in other families of the dicotyledons.

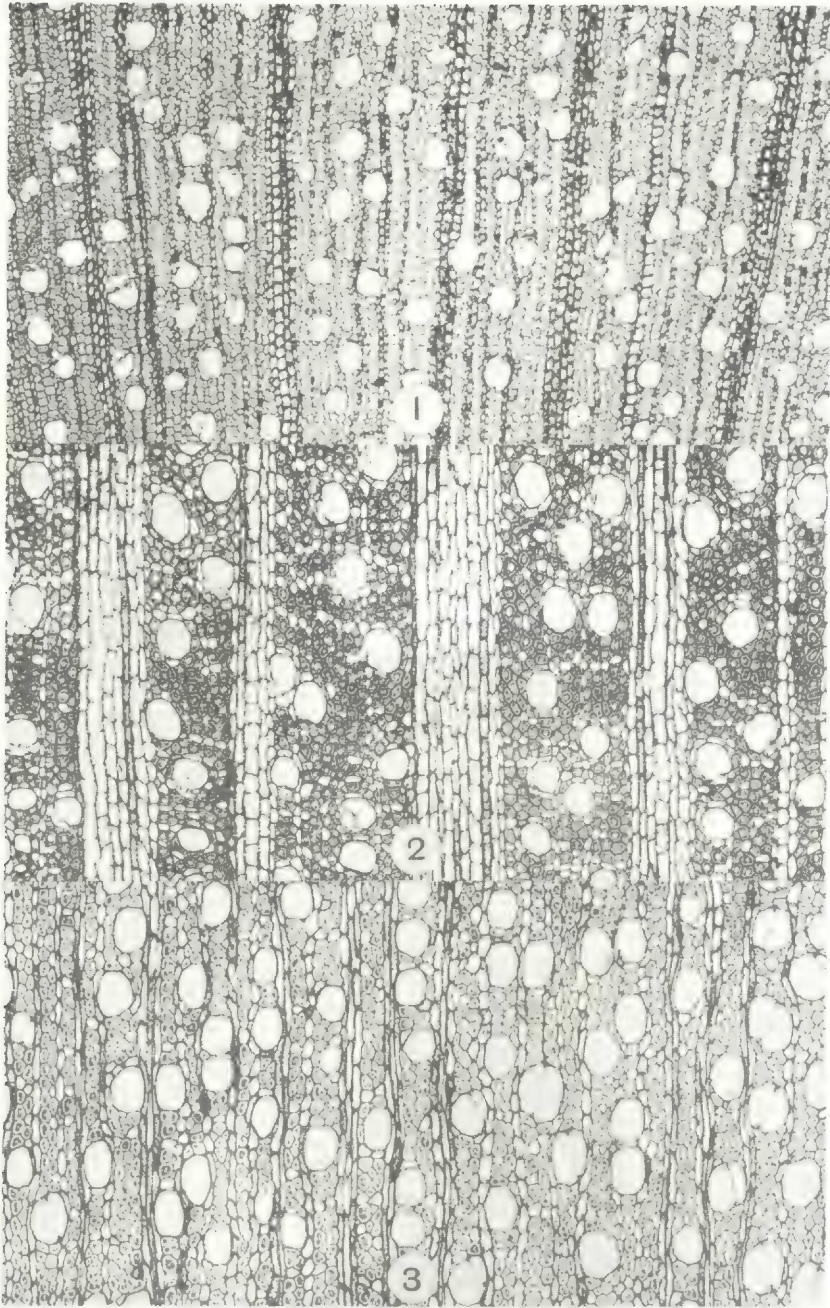
2. These lines of phylogenetic specialization tend in general to be more or less closely correlated and may be utilized in differentiating the Icacinoidae into successive levels of increasing structural modification.

3. For the present, it is not advisable to attempt to subdivide the Icacinoidae upon this basis into more than three major categories: (I) those having vessels with exclusively scalariform perforations, (II) those having scalariform-porous perforations in the vessels of the secondary xylem and (III) those having exclusively porous perforations in the secondary body.

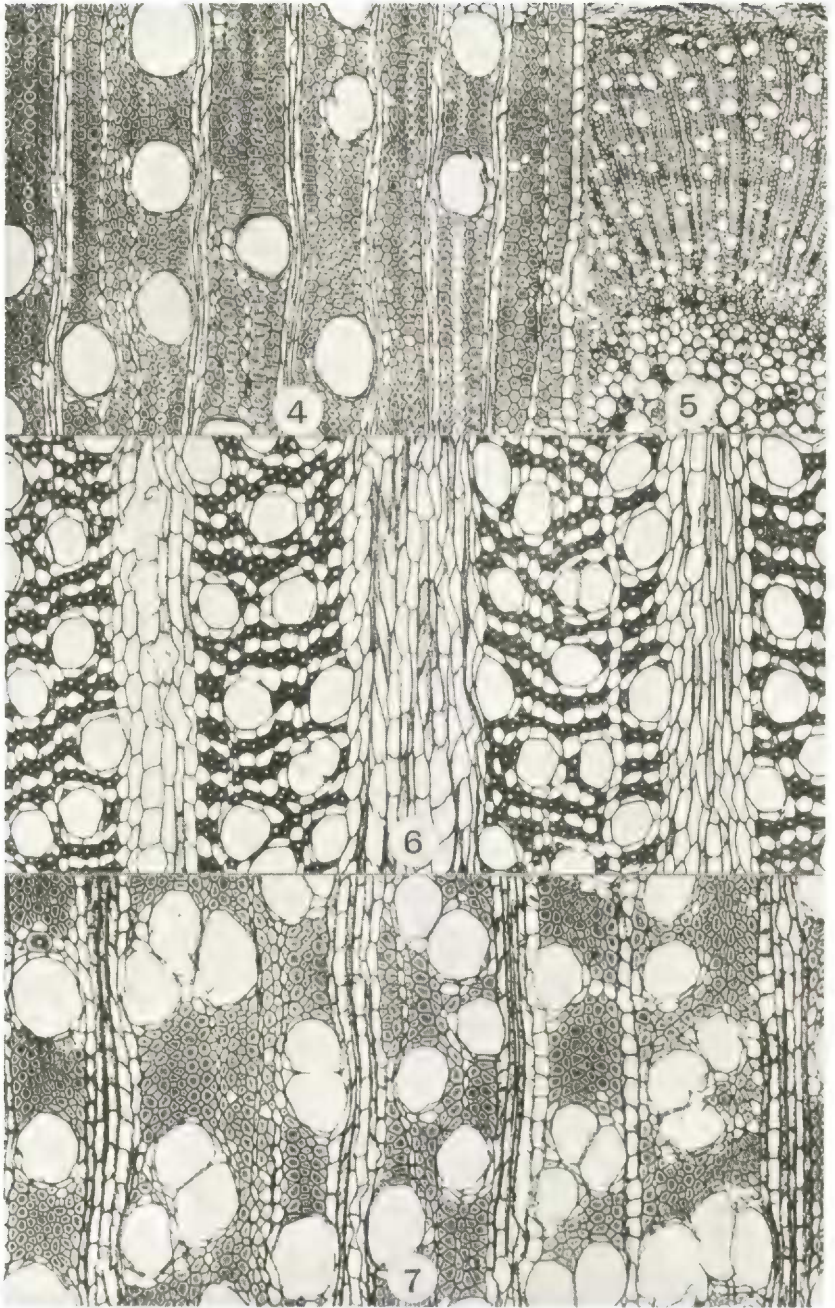
4. It is significant in this connection that the unilacunar Icacinaceae — which were differentiated in the first paper of this series — occur together with the unilacunar Iodeae, Sarcostigmateteae and Phytocreneae in our third category of the Icacinoidae.

LITERATURE CITED

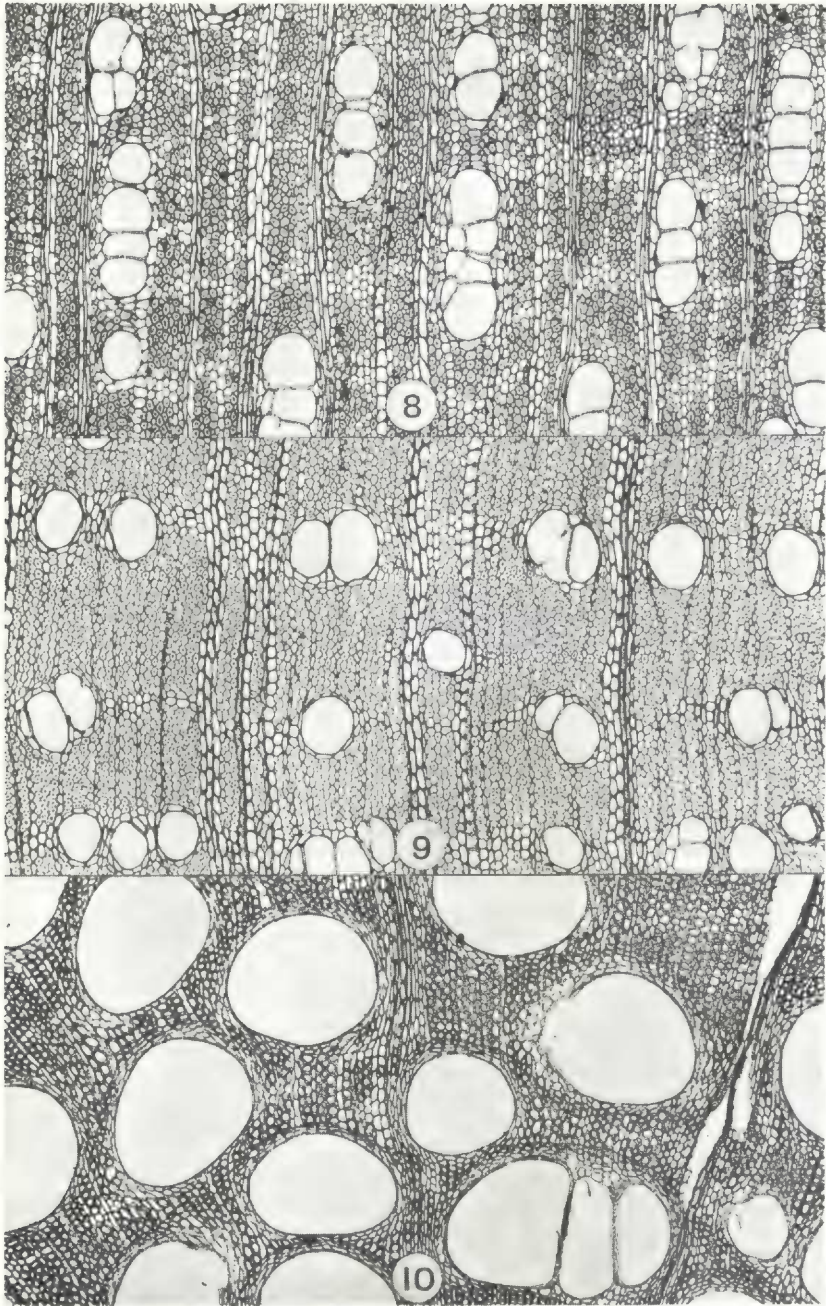
1. BAILEY, I. W. The cambium and its derivative tissues. IV. The increase in girth of the cambium. *Amer. Jour. Bot.* **10**: 499-509. 1923.
2. BAILEY, I. W. AND W. W. TUPPER. Size variations in tracheary cells. I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. *Proc. Amer. Acad. Arts and Sciences.* **54**: 149-204. 1918.



COMPARATIVE MORPHOLOGY OF THE ICACINACEAE



COMPARATIVE MORPHOLOGY OF THE ICACINACEAE



COMPARATIVE MORPHOLOGY OF THE ICACINACEAE